

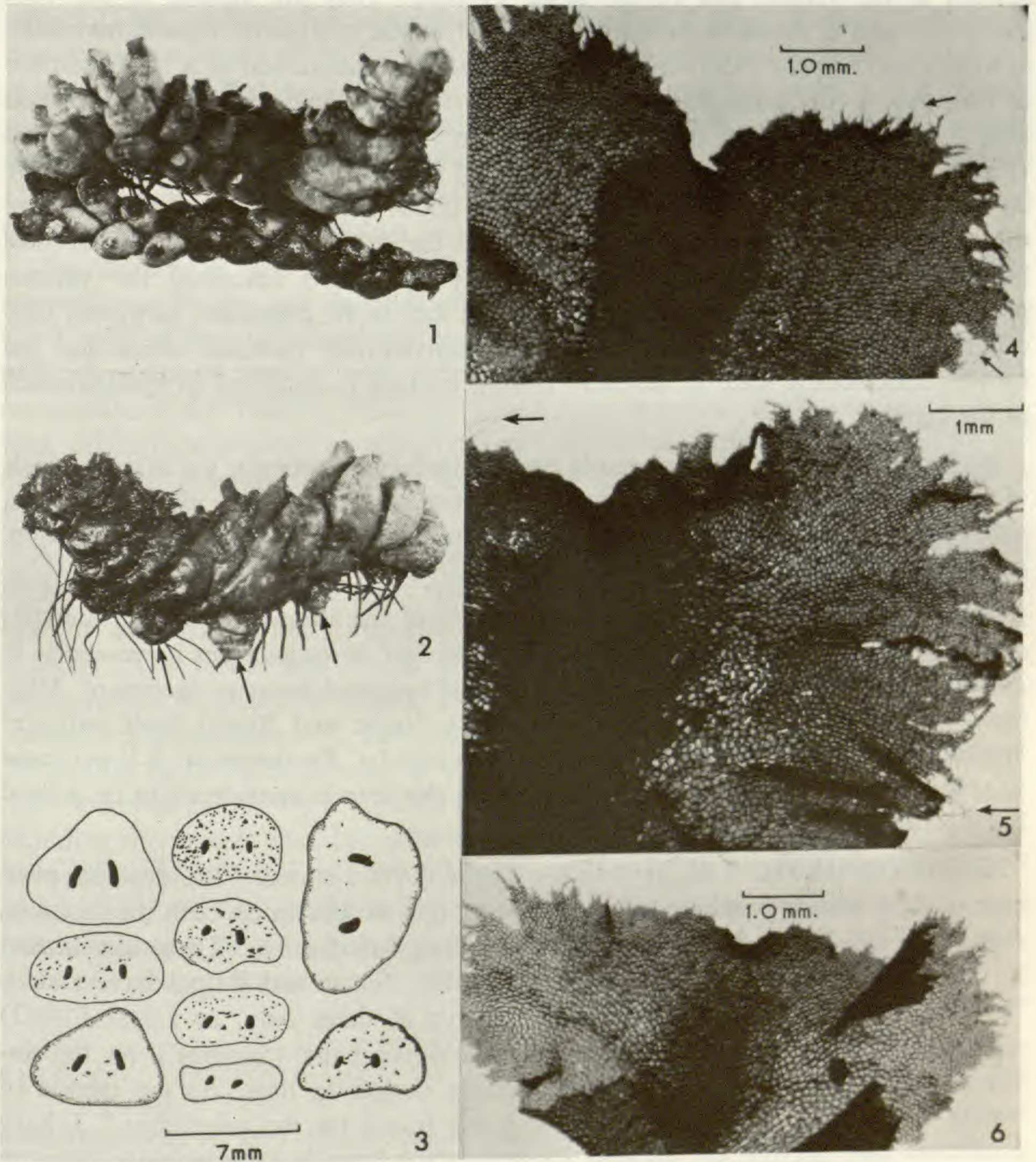
Morphology of *Hypodematium crenatum* (Forsk.) Kuhn: Comments on a Recent Paper

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Some observations dealing with cytomorphology of *Hypodematium crenatum* and phylogenetic relationships of the genus were published a few years ago by Mehra and Loyal (1956) and by Loyal (1960). Japanese material of this species was studied by Hayata (1927) and Iwatsuki (1964). Nayar and Bajpai (1970) have pointed out some "discrepancies" in the observational data published both from this laboratory and also by Iwatsuki. In the following paragraphs comments will be made upon the "discrepancies" noted by Nayar and Bajpai in the papers referred to above.

SYMMETRY OF THE SHOOT AND PHYLLOTAXY.—The shoot and its vascular system, as we recorded, show dorsiventral symmetry. In regard to phyllotaxy it was reported: "the fronds are borne together on the dorsal side. The insertions tend to form diagonal as well as longitudinal rows without any regularity." Nayar and Bajpai quote Iwatsuki (1964) as saying, "two alternating rows" of leaf gaps occur in the Japanese material. Nayar and Bajpai have made no mention of the arrangement of leaves in their morphological description of the rhizome. However, on the basis of the position of leaf gaps in the stelar system, the only arrangement in this fern inferred by them is "three irregular rows" of leaves. The "discrepancy" they noted in our and Iwatsuki's descriptions in fact represents variations of rhizomes of different ages collected from rock-crevices (*Fig. 1*). The variations observed in a given sample may be attributed to the age factor, as well as to the shape and size of the rock crevices. The latter, extrinsic factor also imposes a wide range of variation not only on the form of the basal, swollen part of the stipe but also on the distribution of mechanical cells in its ground tissue (*Fig. 3*). Both these attributes of the stipe are usually constant in ferns growing in uniform, non-restrictive substrata. Secondly, there is abundant evidence available in the literature to show that variations in leaf number and their arrangement in different individuals of the same species or different parts of the same shoot reflect organogenic activity of the perennial meristem in response to factors operating within the meristem and its environments. Bierhorst (1971) has shown in *Equisetum* that the production of an abnormally large leaf in a whorl initiates spiral phyllotaxy in some shoots, in contrast to the whorled arrangement generally known in the Equisetales. Thirdly, at no stage did we question the spiral phyllotaxy in this fern. Our use of the expression, "irregular rows" (or "two alternate rows" by Iwatsuki) is quite appropriate since the spiral phyllotaxy in dorsiventral shoots (e.g., of the heterophyllous species of *Selaginella*) has been described in morphological texts as being in rows.

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Hypodematium crenatum. Fig. 1. Rhizomes of similar length from different rock crevices showing leaves in three rows (above) and two alternate rows (below), ca. $\times 0.5$. Fig. 2. Showing leaves in three rows (above) and two alternate rows (below), ca. $\times 0.5$. Arrested buds (arrows) seen in close proximity to the basal part of the petioles, ca. $\times 0.5$. Fig. 3. Transverse sections of the swollen part of the stipes from different plants. Note variations in the orientation of leaf-trace strands and mechanical tissue (stippled), $\times 5$. Fig. 4. Portion of adult haploid prothallus (arrows indicate acicular hairs). Fig. 5. Same, diploid prothallus. Fig. 6. Portion of adult diploid prothallus showing complete absence of acicular hairs.

POSITION OF THE LATERAL, ARRESTED BUDS.—We described the mode of vascular supply to the lateral buds as follows: "Traces to the buds are associated with the margin of this meristele (ventral)." In their text and Figure 2 Nayar and Bajpai have shown that "the branch traces are profuse and are restricted to the ventral half of the stelar cylinder. They are similar to the root traces . . . and oriented in the same way (not at the margin of ventral meristele, as Mehra and Loyal (1956) reported." A critical reexamination of a large number of rhizomes in my collection shows that the buds originate in close association with the basal regions of the leaves borne on the two lateral sides of the shoot (*Fig. 2*), anatomically two lateral arms of the V-shaped ventral meristele, as we originally stated. The evidence that we have about the sites of bud inception in some ferns is that they normally develop from the detached meristems, their sites being interfoliar (Wardlaw, 1968). Bower (1923) also described the various positions of buds as lateral, basal on the stipe, etc. In *H. crenatum*, however, they occur in between two lateral sides of the dorsiventrally flattened shoot and the root-forming ventral side, an adaptive feature evolved in response to specialization of the habitat.

Nayar and Bajpai have erroneously drawn similarities between the arrested buds of this fern in response to the apical dominance and the stolons of *Nephrolepis*, although the organs are unquestionably distinct in their structural organization, physiology and function.

SORAL ORGANIZATION.—The symmetry of the sorus has been erroneously described as "circular" by Nayar and Bajpai. In fact, it varies from horse-shoe- to J-shaped, or rarely linear, almost similar to that recorded in some species of *Athyrium*. The reniform indusium, as described by Nayar and Bajpai itself indicates zygomorphic symmetry of the sorus rather than circular. Furthermore, it is pertinent to mention that none of the genera with which this fern is considered to be related has a radially symmetrical sorus.

GAMETOPHYTIC TRICHOMES.—Loyal (1960) stated: "Besides the presence of these glands (capitate hairs) on the margin as well as on both the surfaces, some fully-developed gametophytes produce long bristles . . . These are similar to those on the lamina of fronds." Contrariwise, Nayar and Bajpai have stated: "In addition, all the adult prothalli (not some of them only, as Loyal (1960) reported) bear profuse, much elongate, rhizoid-like hairs ('bristles') on the anterior margin and surfaces . . . Acicular hairs similar to those on the lamina of fronds that Loyal (1960) reported were not found on the prothallus." I have confirmed that haploid and diploid prothalli vary from lacking acicular hairs to having quite a few of them (*Figs. 4-5*), even when cultured under uniform conditions of light, nutrition, and space (crowded or not). It should be noted that my cultural conditions are not expected to be the same as those of Nayar and Bajpai. At present no one knows what factors control the presence or absence of the hairs. However, it is conceivable that their initiation may involve some hitherto unthought-of photo-morphogenetic influence which acts after the gametophyte has reached a certain vegetative and/or reproductive phase. As to the variations in

their extent from prothallus to prothallus, it is presumably reflected in their ontogeny, since they develop from the papillate hairs through extension growth. Another variable factor which can hardly be overlooked is the nuclear constitution of the gametophytes. The northwestern Himalayan populations, from which my material came, include diploid, triploid, and tetraploid cytological races. The above-mentioned variations of trichomes were consistently observed both in haploid and in diploid prothallial cultures. The prothalli raised from the spores of the triploid plants showed diverse chromosomal constitution, and, in contrast to the haploid and diploid prothalli, they followed markedly different morphogenetic development (Loyal & Paik, 1971). Most of them failed to develop trichomes comparable to those of the haploid and diploid prothalli.

The difference between the gametophytic acicular hairs (rhizoid-like hairs, according to Nayar and Bajpai) and those of the frond, as they unduly emphasized, may at best be considered one of degree rather than of kind. This is quite understandable in view of their different nuclear constitution. Incidentally, it may be mentioned that Nayar (1956) published a paper earlier which exclusively deals with similarities between gametophytic and sporophytic trichomes. I therefore see no adequate grounds for Nayar and Bajpai to question my observations of a similar kind.

ARCHEGONIAL NECK.—Nayar and Bajpai have recorded: "The archegonial neck is slender and curved away from the apex of the prothallus, the neck is not straight as Loyal (1960) reported." In fact, I described the neck as "almost straight." The whole axis of the archegonium is inclined away from the apical notch (cf. figs. 11, 12 in Loyal, 1960), but in no case was the neck recurved. Nayar and Bajpai seem to have based their conclusion upon a widely-accepted description of the archegonium in advanced leptosporangiate ferns. This assumption, however, cannot be accepted in view of certain recently recorded exceptions, including the present one. In addition, Stone (1961) has described straight-necked archegonia in *Blechnum nudum*, and Atkinson (1967) has reported straight-necked archegonia in *Diplazium expansum*.

Re-evaluation of published data is helpful only provided it is based upon adequate new observations and a deeper understanding of concepts of organization.

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REVIEW

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"INTERMOUNTAIN FLORA. VASCULAR PLANTS OF THE INTERMOUNTAIN WEST, U. S. A., VOL. 1" by Arthur Cronquist, Arthur H. Holmgren, Noel H. Holmgren, and James L. Reveal. 270 pp. 1972. Published by the Hafner Publishing Co., 866 Third Ave., New York, NY 10022. \$17.50.—The Intermountain Region is the semi-desert region of the western United States between the Rocky Mountains on the east and the Sierra Nevada on the west. It is bounded on the north by the high mountains of Idaho and Oregon and on the south by the hot, desert, creosote bush area of Arizona, and so includes all of the state of Utah, most of Nevada, and small parts of Oregon, Idaho, and Arizona. It is thus a natural phytogeographic area rather than an area defined by political boundaries, such as are most floras. This area has been covered by Tidestrom's "Flora of Utah and Nevada," which is now somewhat out of date; since that work had no descriptions or illustrations it was never very usable. The present work, which does have descriptions and fine line drawings of all the species, is the result of many years of study and will provide a definitive account when it is completed. This first volume is mostly devoted to chapters on the physiography of the region, the evolution of the flora, the history of botanical exploration in the region, and the plant geography. The systematic account treats the ferns and fern allies (by Cronquist) and the gymnosperms (by A. and N. Holmgren). Since this is an arid region, ferns are not abundant and are mostly confined to the higher mountains, of which there are several ranges, notably the Uinta and Wasatch Ranges. None of the species is endemic to the area; the rather numerous cheilanthoid ferns are mostly widespread in the western United States, and the others are often widespread subboreal species, sometimes circumboreal. The treatment is carefully prepared and eminently usable. One commendable feature, unusual in floras, is the indication of the types, not only of the accepted species but of the synonyms also. The only error that I have noted is the placing of *Pellaea longimucronata* Hook. as a synonym of *P. truncata* Goodding. This ought to be *P. longimucronata* sensu auctt. non Hook., for Hooker's species is a superfluous and illegitimate substitute name for *P. mucronata*, and by the Code of Botanical Nomenclature (Art. 7) a superfluous name is typified by the type of the name that ought to have been adopted. Therefore the type of *P. longimucronata* Hook. is not *Wright 2131* (New Mexico) but *A. B. Eaton* (California). Students of the ferns of the western United States will surely need to have this volume in their libraries.—C.V.M.